# Is basal metabolic rate associated with recruit production and survival in free-living house sparrows?

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Running headline: Fitness effects of BMR

## Summary

1. Life history theory predicts that available energy is limited and needs to be allocated among different processes such as growth, reproduction and self-maintenance. Basal metabolic rate (BMR), a common measure of an animal's maintenance cost, is therefore believed to be a trait of ecological and evolutionary significance. However, although BMR is often assumed to be correlated with fitness, its association with individual variation in fitness in free-living populations is virtually unknown.

2. We examined the relationship between BMR in late winter prior to the breeding season and recruit production (number of offspring recorded the subsequent year), as well as adult survival, in two populations of house sparrow (*Passer domesticus*) on the islands Leka and Vega in northern Norway.

3. Number of recruits tended to be negatively related to BMR. However, analysing the data for each sex within the two populations revealed that the negative effect of BMR on recruit production was significant only for females on one of the islands.

4. Survival probability was associated with BMR, but the relationship differed both between sexes and populations. In the Leka population, we found evidence for stabilizing selection in the females and disruptive selection in the males. In contrast, there was no effect of BMR on survival in the Vega population.

5. Body mass influenced adult survival, but not recruit production. Furthermore, the relationship between BMR and fitness in females remained significant after controlling for body mass. Thus, the selection on BMR in females was not driven by a BMR-body mass correlation.

6. Basal metabolic rate was significantly related to fitness in both populations. However, the results in the present study show spatial variation as well as sex specific differences in the influence of BMR on fitness in house sparrows.

## Introduction

Basal metabolic rate (BMR) is the lowest level of metabolic output of an endothermic organism in a normothermic state and represents an animal's maintenance cost (McNab 2002). This maintenance cost constitutes between 25 and 40 % of birds total energy expenditure in the field (Bryant 1997) and is therefore believed to be of ecological relevance. Basal metabolic rate shows great variation both between and within species, and the sources of variation have been extensively studied (Burton *et al*. 2011; Konarzewski & Książek 2013; White & Kearney 2013). Variation in BMR between species appears to be linked to basic life history characteristics. For example, tropical birds located at the slow end of the slow-fast continuum of life history variation (Sæther & Bakke 2000) are characterized by a low BMR compared to birds living in temperate environments belonging to the opposite end of the life-history continuum (Wiersma *et al*. 2007; Williams *et al*. 2010). At the intraspecific level common garden studies on passerine birds have shown differences in BMR between populations originating from different climates (e.g. Wikelski *et al*. 2003; Broggi *et al*. 2005; Maggini & Bairlein 2013), indicating an adaptive variation in BMR (Furness, 2003). Furthermore, avian (Rønning *et al*. 2007; Nilsson, Åkesson & Nilsson 2009; Tieleman *et al*. 2009; Bushuev, Kerimov & Ivankina 2011; Mathot *et al*. 2013) as well as mammalian (Konarzewski, Książek & Łapo 2005; Sadowska *et al*. 2005; Wone *et al*. 2009; Boratyński *et al*. 2013) studies provide growing evidence for significant additive genetic variance in this trait. These finding are further supported by the fact that BMR responds to artificial selection

(e.g. Książek, Konarzewski & Łapo 2004). However, in spite of being a trait that has been found to exhibit additive genetic variation and been shown to respond to selection, the link between BMR and fitness is still poorly understood.

The sign of the relationship between BMR and individual fitness, if any, is not obvious and arguments have been put forward for either a positive or a negative relationship. According to life history theory, available energy is limited and a fixed resource budget needs to be allocated between various biological processes such as growth, reproduction and self-maintenance (Gadgil & Bossert 1970; Roff 1992; Stearns 1992). Consequently, individuals with low BMR should perform better because their lower self-maintenance cost enables them to allocate more energy towards fitness-enhancing processes like growth and reproduction. Hence, a negative relationship between BMR and reproduction should exist ('compensation' hypothesis; Nilsson 2002). On the other hand, it has been argued that the ability to support a high level of activity requires morphology with a high maintenance cost, i.e. high BMR (e.g. Bennett & Ruben 1979; Hayes & Garland 1995). A high BMR is often associated with large internal organs, including the alimentary tract (Lindström & Kvist 1995; Chappell, Bech & Buttemer 1999). Individuals with high BMR may therefore have the capacity to eat more food and convert it into usable energy at a higher rate. Basal metabolic rate has in turn been found to correlate with total energy expenditure in free-living birds (Daan, Masman & Groenewold 1990), but see Ricklefs, Konarzewski & Daan (1996). If BMR is functionally linked to working capacity, a positive relationship between BMR and reproduction should be expected ('increased intake' hypothesis; Nilsson 2002).

Although studies on the relationship between energy metabolism and fitness are few (Burton *et al.* 2011), some evidence is now accumulating that BMR is related to differences in reproductive success of birds. For instance, in male Leach's storm-petrels (*Oceanodroma leucorhoa*) individuals with low BMR during the incubation period produced more offspring

by starting breeding earlier in the season (Blackmer *et al*. 2005). Conversely, Chastel, Lacroix & Kersten (2003) found that house sparrows (*Passer domesticus*) with high pre-breeding plasma triiodothyronine levels, a hormone related to BMR in the studied population, raised more offspring. However, in great tits (*Parus major*) Bouwhuis *et al*. (2014) found no evidence for directional selection on BMR when using the number of offspring produced during the breeding season as a measure of fitness. Instead males with an average BMR produced more offspring. Studies on laboratory rodents suggest that reproductive performance is unrelated to BMR (Derting & McClure 1989; Hayes, Garland & Dohm 1992; Johnson, Thomson & Speakman 2001; Johnston *et al*. 2007). To our knowledge only one study has investigated the association between reproduction success and BMR in a free-living mammal population, where Boratyński & Koteja (2010) found that BMR was positively associated with overall reproductive success in the bank vole (*Myodes glareolus*).

In the only study investigating the association between BMR and survival in a free living bird population; Bouwhuis *et al*. (2014) found no relationship between winter BMR and survival in great tits. However, in mammals, Larivée *et al*. (2010) found evidence for negative selection on resting metabolic rate, a trait closely related to BMR, in juvenile North American red squirrel (*Tamiasciurus hudsonicus*), whereas selection in the opposite direction has been found in short tailed voles (*Microtus agrestis*; Jackson, Trayhurn & Speakman 2001). Furthermore, BMR was found to affect over-winter survival in two geographically separated bank vole populations, but the selection on BMR differed both between sexes and seasons (Boratyński & Koteja 2009; Boratyński *et al.* 2010).

Results from studies investigating the relationship between variation in BMR and life history and behavioural parameters important for individual fitness provide inconclusive evidence for BMR as an important fitness-related trait (Biro et al. 2010; Burton *et al*. 2011; Šíchová et al. 2014). Furthermore, much of our knowledge is based on studies conducted on

animals in captivity which may not be representative of free-living animals, which most likely are facing different trade-offs between reproduction and other energy consuming tasks like foraging, thermoregulation and predator avoidance. Hence, within the field of evolutionary physiology there is great need for empirical studies on fitness consequences of individual variation in BMR in free-living populations. In the present study we therefore examined the relationship between BMR and important components of fitness in free-living populations of a passerine bird. We measured BMR in adult house sparrows in late winter prior to the breeding season. As a measure of fitness, we used number of recruits recorded the subsequent year and adult survival to the next winter. First, we investigated whether natural selection acted on BMR with respect to recruit production, by testing whether the relationship was directional (as predicted by the 'compensation' and 'increased intake' hypothesis), versus nonlinear (indicating stabilizing or disruptive selection). We then investigated whether natural selection acted on BMR with respect to adult survival from one season to the next. Whole body BMR, i.e. not controlled for the effect of body mass, is used in an ecological context as a predictor of the cost of living (e.g. Tieleman *et al.* 2009), and is consequently a potential target of selection. However, because body mass may influence both BMR and fitness, we also fitted models which included body mass, in order to examine the residual effect of BMR on fitness.

## Materials and methods

### STUDY SPECIES AND STUDY AREA

The study was conducted in 2007 and 2008 using two house sparrow (*Passer domesticus*, Linnaeus, 1758, Fig. 1) populations living on the islands Leka (65.1 ºN 11.6 ºE) and Vega

(65.7 ºN 11.9 ºE) off the coast of northern Norway. These populations are included in a long term study and nearly all birds (>90%) present on the two islands have been captured and banded annually during winters 2002-2014. The house sparrows on these islands live in close proximity to human settlements, and usually nest and seek shelter inside barns and cowsheds. Birds were captured by mist-netting inside or close to farm buildings. Each bird was banded with a metal ring, and a unique combination of coloured plastic rings to allow identification with telescopes. To allow easier estimation of the overall proportion of birds captured during the study, birds were continuously transferred to an empty barn (from now on referred to as aviary) where they were provided water and food (bread, grain, grain feed and sunflower seeds) *ad libitum*. After the experiment period, birds were released at the same location as they were captured.

## MORPHOLOGICAL AND PHYSIOLOGICAL MEASUREMENTS

Body mass was measured with a Pesola spring balance (to the nearest 0.1 g.). A small blood sample (~25 µL) was collected from the brachial vein and stored on 96% ethanol for later DNA genotyping. In 2007 measurements of BMR were obtained for 105 individuals on Leka during the period 13-27.02 and for 89 individuals on Vega during the period 2-15.03.

Basal metabolic rate was measured as oxygen consumption rates using an open flow system. Dried outside air was pumped (500 mL $min^{-1}$) through four metabolic chambers (1.1 L) located inside a climate cabinet at ca. 30.5 ºC, i.e. within the thermoneutral zone for the house sparrow (Hudson & Kimzey 1966). Air flow into the chambers was adjusted using calibrated Bronkhorst High-Tech mass flow meters (Ruurlo, The Netherlands), and a Servomex type 4100 two-channel oxygen analyser (Crowborough, England) measured the oxygen concentration in dried effluent air. An automatic valve-system switched between two

and two chambers (every 30 min), and the voltage output from the oxygen analyser, the flow meters and thermocouples inside the metabolic chambers were stored every 30 s. on a Grant Squirrel, type 1200 data logger (Cambridge, England). The baseline gas level (without birds in the chambers) was recorded for one hour before and after each trial to enable correction for linear analyser drift during the measurement period. The rate of oxygen consumption ($VO_2$) was calculated following Withers (2001), using a respiratory quotient of 0.71. The lowest 10 min running average $VO_2$ value was used to represent BMR.

To reduce time spent in aviaries, birds were measured in two sessions per day, either in the evening between 16:00 and 22:30 local time, or during the night from 23:00 to 08:00. Note that in northern Norway day length is short in February and March. The average daily light cycle during the measurement period was 10L:14D (light: 07:30 - 17:30 local time). Consequently, the birds were measured during their normal resting phase, irrespectively of whether they were measured late in the evening or during the night.

Birds were captured at different locations around the islands between 10:00 and 15:00, and from these birds we selected eight individuals to be measured the same day, while the rest of the birds were transferred to the aviary to be recaptured and measured another day. Thus, some birds were measured before they were put in the aviary, while other birds were measured after spending some days inside the aviary (mean 6 days; range 1-14 days).The birds went through the same experimental protocol irrespective of whether they were processed the same day as they were captured or if they were recaptured (around 15:00) inside the aviary. Four birds were placed directly in the metabolic chambers for metabolic measurements, whereas the remaining four birds were placed in individual cages until the start of their measurements at 23:00. To ensure that the birds held in cages did not starve, but at the same time reached a post absorptive state during measurement, they were supplied with a small piece of moist bread while in the cage. Immediately after the birds were taken out of

the metabolic chamber they were released into the aviary in a section separated from birds not yet measured.

Both measurement duration and circadian rhythm may affect physiological variables (Page, Cooper & Withers 2011). However, neither number of days inside the aviary before measurement nor measurement period (evening or night) affected oxygen consumption significantly (Table S1 in Supporting Information). Thus, the metabolic measurements are referred to as BMR regardless of being obtained in the evening or during the night.

Descriptive statistics of BMR and body mass are given in Table 1.

## ESTIMATION OF FITNESS COMPONENTS

None of the birds measured for BMR in 2007 and assumed to be dead in 2008 were observed in a subsequent year (until 2014). Thus, we are confident that a bird not observed during field work in 2008 could be considered dead and we did not account for recapture rate in the analyses (Lebreton *et al.* 1992). Furthermore, due to the high recapture rate in the study system, we assumed that any unmarked bird captured in the winter was born the previous year. These individuals were considered as being recruits to the breeding population and were included as recruiting offspring in the calculations of reproductive success of putative parents (i.e. previously marked birds). No data was collected during the breeding season. Thus, data on e.g. number of eggs and fledglings is not available. A detailed description of the genetic analysis and determination of parentage is provided in Appendix S1 in Supporting Information. In short, birds were genotyped using 14 highly polymorphic microsatellite markers. Microsatellite markers were amplified using polymerase chain reaction (PCR) and their alleles separated by electrophoresis in an automated 16 capillary ABI Prism 3130xl Genetic Analyser (Applied Biosystems, USA). Individual alleles at each microsatellite locus

were scored using the software GENEMAPPER 4.0 (Applied Biosystems, USA). The parentage analysis software CERVUS version 3.0 (Kalinowski, Taper & Marshall 2007) was used to determine the genetic parentage. All adult birds present on the islands in February/March 2007 were classified as potential parents of any unmarked birds captured during the 2008 field season assumed to be recruits from the previous breeding season. On Leka, we identified the genetic father for 66.7% and the genetic mother for 69.2% of the recruits. On Vega 62.3% and 81.2% of the recruits was assigned a genetic father and mother, respectively.

## STATISTICS

Variation in BMR was analysed in a generalized linear model (GLM) including body mass, age, number of days in aviary, island (population), sex and measurement period (evening or night) as explanatory variables. To test for differences between sexes and populations in the effect of the other predictor variables, two- and three-way interactions between sex, island and the other variables were included. The effect of BMR on fitness was examined in two stages. First we tested for differences in selection between the populations and sexes by investigating the effect of BMR on fitness (number of recruits and survival) in the pooled data by including the linear and quadratic effects of BMR and the two- and three-way interactions between sex, island and BMR. Secondly, linear and quadratic effects of BMR on fitness were analysed separately for each sex in the two populations. Furthermore, as variation in BMR was explained by body mass and age, we also examined the partial effect of BMR on fitness by including body mass (measured shortly after the birds were captured) and age in the models. To remove the correlation between linear and quadratic terms, values of BMR and body mass were mean-centred within all birds in the pooled data analysis and

within the sexes in each population in the separate analysis. The models investigating the effect on recruit production for the pooled data and for the males from both Leka and Vega showed evidence of over-dispersion ('dispersiontest', R package AER, Kleiber & Zeileis 2008). Consequently, we applied negative binomial generalized linear models with a log link using the function 'glm.nb' (including a parameter to model over-dispersion) in the R package MASS (Venables & Ripley 2002). In females, number of recruits were analysed using GLMs with a Poisson error distribution and a log link. The association between BMR and survival was tested in a logistic regression, using a binomial GLM with a logit link function. Survival was coded as a binary variable; alive the subsequent year (1) or not (0). Note that standardized selection differentials and gradients, calculated following Lande & Arnold (1983), are given in Supporting Information to allow for comparison of strength of selection with other studies (Table S4). All statistical analyses were performed in R ver. 2.15.3 for Windows (R Development Core Team 2013).

## Results

RECRUIT PRODUCTION

In the analysis including all individuals, BMR tended to be negatively associated with recruit production ($\beta = -0.022$, $\chi^2_1 = 3.777$, $P = 0.052$, Table S2 in Supporting Information). However, when analysing the data separately for each sex on each island, the relationship between BMR and recruit production was only apparent in females. For females in the Vega population, we found that lower BMR was associated with higher recruit production (Fig. 2). Furthermore, the negative effect of BMR on number of recruits produced by the females on Vega was significant also when controlling for body mass (Table 2). In the Leka population,

there was no significant linear relationship between BMR and recruit production, but females with an intermediate BMR tended to produce more recruits as indicated by the quadratic term (Fig. 2). The second-order effect was reduced when body mass was included in the model, indicating that the apparent selection on BMR was partly mediated through indirect selection on body mass (Table 2). In males, BMR did not influence number of recruits in any of the two populations studied (Fig. 2, Table 2). Although the effect of BMR on recruit production differed slightly between the sexes and populations (Fig. 2), the slopes did not differ significantly (Table S2). Furthermore, neither body mass nor age affected recruit production significantly in any sex in the populations studied (Table 2)

SURVIVAL

The linear and quadratic effect of BMR on survival differed between the sexes, as well as between the populations (Table S2). We found no evidence for an effect of BMR on survival on Vega, in neither sex. This was true both without (Fig. 2) and with body mass in the models (Table 2). In the Leka population, there was no significant linear relationship between survival and BMR. Instead, for the females we found a negative quadratic effect of BMR on survival (Fig. 2). Furthermore, after controlling for body mass, the quadratic effect of BMR on survival in the females was still highly significant (Table 2). For the males on Leka survival tended to be higher in individuals with high and low BMR (Fig. 2). When controlling for body mass, the positive quadratic relationship between survival and BMR was significant (Table 2), indicating disruptive selection on BMR which was independent of body mass.

In contrast to recruit production, survival was related to body mass. In the Vega population, there was a linear effect of body mass on survival, but the direction of selection

differed between the sexes. In females the probability of survival decreased with increasing body mass, whereas in males survival probability increased with body mass (Table2). In males on Vega survival also increased with age (Table 2). For females in the Leka population, survival probability increased with increasing body mass, whereas for males we found evidence for stabilizing selection on body mass based on survival from 2007 to 2008 (Table 2).

## Discussion

This study has demonstrated different patterns in the influence of BMR on both survival and fecundity in two populations of house sparrows. In the population on Vega, BMR was negatively related to recruit production in the females, and this relationship was present also after controlling for body mass. Hence, the effect of BMR on recruit production was not driven by indirect phenotypic influence of body mass. This implies that females with low maintenance cost independent of body mass invested more energy into reproduction, compared to high BMR females. This finding is in contrast with a previous study of house sparrows further south (46.1 ºN) where individuals with high BMR prior to breeding season produced more offspring, mainly as a consequence of starting breeding earlier in the season and having more clutches (Chastel, Lacroix & Kersten 2003). Unfortunately, we cannot determine whether individual differences in the number of recruits produced are due to variation in the number of fledglings produced, differences in survival from fledging to recruitment, or a combination of these factors. However, number of fledglings has previously been shown to be a good predictor for number of recruits in passerine birds (e.g. Grant & Grant 2000), making differences in number of fledglings produced the most plausible explanation. In the Leka population there was no directional association between BMR and

312 production of recruits. Instead, females with an average BMR tended to produce more
313 recruits. Stabilizing selection on mass-corrected BMR based on number of hatchlings
314 produced has previously been found in free-living passerines (Bouwhuis *et al*. 2014).
315 However, when controlling for body mass in the present study the tendency of a stabilizing
316 selection on BMR was weakened, which may suggest that the influence of BMR was partly
317 driven by the correlation with body mass.
318 Basal metabolic rate is known to be a flexible trait, and to test the 'compensation' and
319 'increased intake' hypothesis metabolic measurements should ideally been obtained during
320 the energetically challenging breeding period. However, we measured BMR in February and
321 March, approximately 1.5-2 months before the start of the breeding season in these
322 populations (Kvalnes *et al.* 2013). Basal metabolic rate is generally found to be a repeatable
323 trait (Nespolo & Franco 2007). Thus, when discussing our results on the association between
324 BMR and recruit production, we assume that differences in BMR found among individuals
325 prior to the breeding season partly reflects differences in maintenance cost during breeding
326 (but see Bouwhuis, Sheldon & Verhulst 2011). The directional negative relationship between
327 BMR and reproduction found in the present study indicates that individuals with low
328 maintenance cost were able to devote more energy to reproduction, which supports the
329 'compensation' hypothesis (Gadgil & Bossert 1970; Nilsson 2002). However, although BMR
330 tended to have a negative effect on recruit production in the house sparrows, we have to
331 emphasize that this was only significant in females in one of the study populations. In
332 agreement with a previous study conducted in four Norwegian house sparrow populations
333 showing no effect of body mass on total recruit production measured as lifetime reproductive
334 success (Jensen *et al*. 2004), body mass was not found to be a significant predictor for recruit
335 production in any of the sexes in neither population in the present study (see also Jensen et al.
336 2008). Furthermore, although reproductive performance in birds is known to improve with

age (e.g. Forslund & Pärt 1995), we found no effect of age on recruit production in our study populations.

We found no evidence for a directional association between BMR and survival. This agrees with another study on a free-living passerine species, showing no effect of BMR on survival of great tits (Bouwhuis *et al*. 2014). Contrary to the study on great tits, we found evidence for a nonlinear relationship between BMR and survival in the house sparrows. In the Leka population, the selection on BMR was stabilizing in the females, but disruptive in the males. The fact that females with an average BMR were more likely to survive indicates that there could be trade-offs between costs (e.g. compromised immunocompetence: Książek *et al*. 2007) and benefits (e.g. increased cold tolerance: Liknes & Swanson 1996) of having a high BMR. Based on the data in hand, we are unable to determine the underlying reasons for why such trade-offs do not seem to apply for females on Leka and neither sex on Vega. Nevertheless, because the house sparrows in our study populations spend much time inside barns during the winter, they may not face trade-offs to the same degree as wintering forest species which typically experience low temperatures as well as low food predictability (Broggi *et al.* 2004).

The main predictor of survival in the house sparrow populations studied was body mass. In the house sparrow population on Vega selection on body mass operated in opposite directions in the sexes, being positive in the males and negative in the females. A difference between the sexes was also found in the Leka population where an increase in survival with increasing body mass was observed for females, whereas a stabilizing selection on body mass was observed for males. Sexual differences in selection on body mass was not found in a previous study of house sparrows living on the coast of northern Norway, which found body mass to be positively related to survival in both sexes (Jensen *et al.* 2008). The effect of body mass on fitness was not the main objective of the present study. Nonetheless, our results

indicate that costs and benefits of high body mass probably differed between the sexes, and that this resulted in different relationships with survival. Furthermore, an interesting observation in the Leka population was that the effects of body mass and BMR on male survival differed indicating that these traits may evolve in different directions. This is however depending on both traits being heritable and exhibiting independent additive genetic variance (e.g. Lynch & Walsh 1998).

In the present study we found evidence for a link between BMR and fitness, but this was more pronounced in female house sparrows. Although, studies investigating the link between BMR and fitness in free-living population are scarce, sexual differences in the association between BMR and fitness related components have been shown earlier in avian studies (Blackmer *et al.* 2005; Bouwhuis *et al.* 2014). Furthermore, selection on BMR has been found to differ both between sexes and seasons in free-living rodents (Boratyński & Koteja 2009, 2010). Hence, several studies (including the present) investigating the association between BMR and life history parameters important for individual fitness have failed to find a general pattern. Based on this observation one could argue that a single optimal BMR probably does not exist. However, it has to be mentioned that most studies investigating the link between BMR and fitness are correlative studies measuring the effect of BMR on short-term fitness. Fitness relationships may also be revealed by manipulating genetic architecture (Ketola, Boratyński & Kotiaho 2014; see also Abbott 2014). Evidence from studies using this approach is still limited, but suggests that the predominant direction of past selection on BMR in e.g. bank voles has been negative (Ketola, Boratyński & Kotiaho 2014; Boratyński *et al.* 2013). Thus, at present we cannot exclude the possibility that there might be a general trend of limiting maintenance cost which correlative studies measuring short-term fitness effects fail to reveal. Nevertheless, it has been proposed that the association between BMR and fitness probably varies temporarily and spatially depending on

environmental factors such as e.g. food availability, predator abundance and temperature (Mathot *et al*. 2009; Boratyński & Koteja 2010; Larivée *et al.* 2010; Burton *et al*. 2011). Looking at morphological traits, changes in direction of selection are frequently observed in nature (e.g. Siepielski, DiBattista & Carlson 2009). More studies are needed to determine if this also apply to physiological traits like e.g. BMR. However, the persistence of large variation in BMR between and among species indicates that it is unlikely to be a single metabolic phenotype which is favourable under all environmental conditions. Thus, the effect of different stochastic environmental factors on the association between metabolic traits and fitness warrants further investigation.

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## Data Accessibility

411 All data are included in the manuscript and supporting information.

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413 ## References

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## Supporting Information

Additional supporting information may be found in the online version of this article.

**Appendix S1:** Description of the genetic analysis and determination of parenthood

**Appendix S2:** Data used in the study

**Table S1**: Sources of variation in BMR

**Table S2:** Relationship between BMR and fitness (pooled data)

**Table S3:** Relationship between BMR and fitness (separately for island and sex)

**Table S4:** Standardized selection differentials and gradients for BMR and body mass.

616 Table 1. Descriptive statistics of basal metabolic rate (BMR) and body mass in house
617 sparrows from Vega and Leka, Norway.

| | | Females | | | | Males | | | |
|---|---|---|---|---|---|---|---|---|---|
| Population | Trait | *N* | *Mean* | *S.D.* | *Range* | *N* | *Mean* | *S.D.* | *Range* |
| Vega | BMR (mL $O_2$ $h^{-1}$) | 39 | 77.54 | 9.04 | 53.46 - 98.61 | 50 | 79.53 | 9.50 | 58.24 - 96.95 |
| | Body mass (g) | 39 | 30.76 | 1.73 | 27.50 - 33.90 | 50 | 31.67 | 2.12 | 26.60 - 37.70 |
| Leka | BMR (mL $O_2$ $h^{-1}$) | 52 | 82.73 | 6.77 | 67.08 - 96.18 | 53 | 81.51 | 7.32 | 62.85 - 97.82 |
| | Body mass (g) | 52 | 31.81 | 2.04 | 27.50 - 36.90 | 53 | 32.01 | 1.45 | 28.80 - 35.00 |

618

619 Table 2. The association between basal metabolic rate (BMR, mL $O_2$ $h^{-1}$), body mass (g), age
620 (years) and components of fitness in two populations of house sparrows in northern Norway.

| Population | | Recruit production* | | | Survival† | | |
|---|---|---|---|---|---|---|---|
| VEGA | Predictor variables | Estimate | $\chi^2_1$ | *P* | Estimate | $\chi^2_1$ | *P* |
| Females | Intercept | **0.755** | **7.553** | **0.006** | 0.985 | 0.617 | 0.432 |
| (N = 39) | BMR | **-0.034** | **6.281** | **0.012** | 0.011 | 0.066 | 0.797 |
| | $BMR^2$ | -1e-4 | 0.160 | 0.690 | 1e-4 | 0.002 | 0.967 |
| | Body mass | -0.011 | 0.026 | 0.873 | **-0.528** | **5.498** | **0.019** |
| | Body $mass^2$ | -0.033 | 1.095 | 0.295 | 0.018 | 0.023 | 0.878 |
| | Age | 0.137 | 0.967 | 0.325 | -0.528 | 1.165 | 0.280 |
| Males | Intercept | -0.332 | 0.570 | 0.450 | **-1.807** | **4.289** | **0.038** |
| (N = 50) | BMR | -0.015 | 0.271 | 0.603 | -0.067 | 1.854 | 0.173 |
| | $BMR^2$ | 0.002 | 0.692 | 0.406 | 0.005 | 1.525 | 0.217 |
| | Body mass | 0.114 | 0.658 | 0.417 | **0.839** | **11.162** | **<0.001** |
| | Body $mass^2$ | 0.015 | 0.194 | 0.660 | -0.039 | 0.187 | 0.666 |
| | Age | 0.203 | 1.411 | 0.235 | **0.986** | **4.870** | **0.027** |
| LEKA | | | | | | | |
| Females | Intercept | -0.762 | 2.538 | 0.111 | 0.561 | 0.465 | 0.495 |
| (N = 52) | BMR | -0.017 | 0.163 | 0.687 | 0.047 | 0.343 | 0.558 |
| | $BMR^2$ | -0.009 | 3.152 | 0.076 | **-0.030** | **10.920** | **<0.001** |
| | Body mass | -0.116 | 1.176 | 0.278 | **0.425** | **4.798** | **0.029** |
| | Body $mass^2$ | 0.019 | 0.309 | 0.578 | -0.010 | 0.022 | 0.882 |
| | Age | 0.093 | 0.213 | 0.645 | -0.157 | 0.207 | 0.649 |
| Males | Intercept | -0.246 | 0.195 | 0.659 | -0.465 | 0.347 | 0.556 |
| (N = 53) | BMR | -0.050 | 1.134 | 0.287 | -0.044 | 0.639 | 0.424 |
| | $BMR^2$ | -0.003 | 0.549 | 0.459 | **0.011** | **5.163** | **0.023** |
| | Body mass | -0.087 | 0.131 | 0.718 | 0.094 | 0.077 | 0.782 |
| | Body $mass^2$ | -0.212 | 2.767 | 0.096 | **-0.427** | **6.264** | **0.012** |

| | | | | | | |
|---|---|---|---|---|---|---|
| Age | -0.013 | 0.002 | 0.968 | -0.194 | 0.206 | 0.650 |

621

622 *Recruit production = number of recruits recorded the subsequent year.

623 †Survival = adults surviving from late winter 2007 to late winter 2008 (1) or not (0).

624

625

626 FIGURE LEGENDS

627

628 Fig. 1. Male house sparrow (*Passer domesticus* Linnaeus, 1758). The bird is banded with a
629 unique combination of coloured plastic rings which enables identification with telescope.
630 Photo: Bernt Rønning.

631

632 Fig. 2. Relationship between basal metabolic rate measured in late winter 2007, number of
633 recruits recorded the subsequent year (left panel) and the probability of survival to the
634 subsequent year (right panel) in house sparrows from Vega and Leka, Norway. Fitted lines
635 represent predicted values for the linear effect (solid lines) or a combination of the linear and
636 quadratic effect (if $P \leq 0.1$; short dashed lines) of BMR. Dotted lines represent the 95%
637 confidence intervals. P-values for the linear and quadratic (underlined) effect of BMR are
638 given. Statistics from models used to calculate the predicted values are shown in Table S3 in
639 Supporting Information.